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# Ecological Aspects of the Distributions of Fishes at Fanning Island[1]

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ABSTRACT: The nearshore marine environment of Fanning Island (3° 55′ N, 159° 23′ W) was subjectively partitioned into seven habitats which are briefly described. Efforts were made to sample in each in order to obtain as complete as possible a record of the fish species present. Observations were made underwater by skin and SCUBA diving during July–August 1972, and April 1973; 214 species of fishes (96 genera in 37 families) were seen. Tables provide semiquantitative abundance estimates for each species in every habitat, and a list of characteristic species associated with various substrates within the habitats. Semiquantitative abundance estimates were used to generate diversity estimates and two measures of faunal resemblance for the habitats taken two at a time. Relationships between the faunas of the different habitats were used to generate hypotheses about ecological relationships between habitats. It is argued that strong surge and tidal currents strongly influence the distributions of Fanning Island fishes, separating outer reef fishes from lagoon fishes by a rich zone associated with the English Harbor channel. Our observations include the addition of 57 species to the Line Islands fish fauna. Their zoogeographical affinities support an earlier determination of a central Pacific character for the Line Islands fishes.

THE FISHES at Fanning Island are mainly Indo-Pacific in origin, and have been characterized as an eastward extension of the central Pacific fauna as typified by the fishes of the Marshall Islands (Gosline 1971). Fanning and the other Line Islands are unusual in that the reef fishes are little exploited, nor is their habitat disturbed, by man. The physical and biological forces acting on the fish fauna are entirely natural ones.

Several early expeditions made fish collections while at Fanning Island. Their scattered reports were compiled by Fowler (1928, 1931, 1934, 1949), but detailed locality records are lacking. In the 1960s J. E. Randall made a limited number of poison stations at Fanning (Randall, personal communication). In 1963 Backus observed effects of grazing fish on algae and invertebrates in Fanning Island Lagoon and in Danger Point Tidepool, and described water conditions and topographical features (Backus 1964). The most recent study of Fanning fishes—two collections by Gosline from the tidepools at Danger Point and North Point—formed the basis for a checklist of inshore fishes (Gosline 1970) and a discussion of zoogeographical affinities (Gosline 1971).

The present study was undertaken to sample more thoroughly the fish fauna of Fanning Island, to provide baseline data for future studies of temporal and geographical variation, and to determine the instantaneous distribution of fishes among the available habitats. Estimates of abundance are presented and an attempt is made to relate our observations to ecological factors.

## MATERIALS AND METHODS

### *Study Areas*

The nearshore marine environment was partitioned into seven habitats on the basis of subjectively perceived discontinuities of bottom physiography and water conditions. Efforts were made to sample within each of these in order to obtain as complete as possible a record of the species present at Fanning Island.

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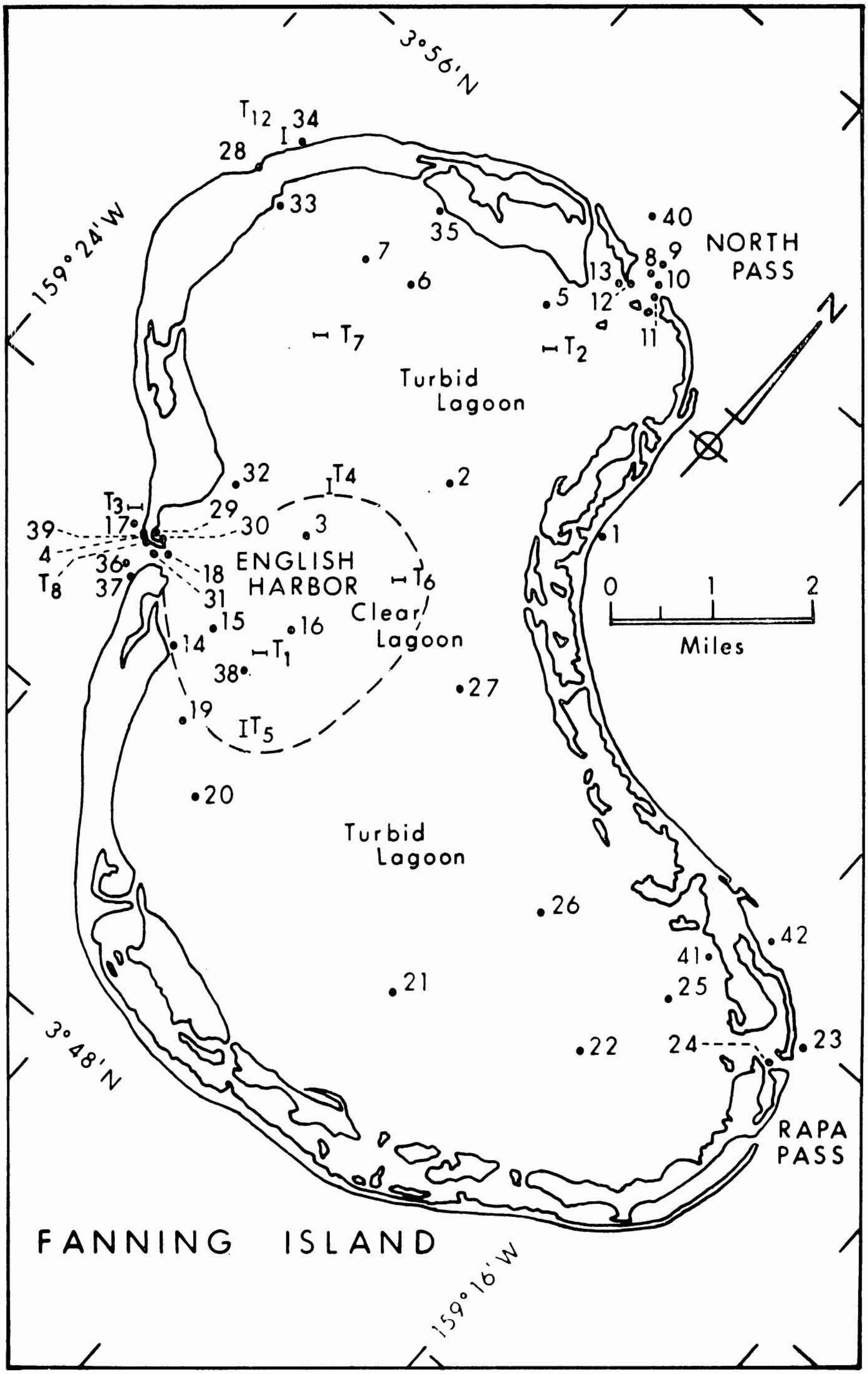


FIG. 1. General distribution of sample sites (numbered dots); short lines labeled $T_1$, $T_2$, etc. represent transect sites. The broadly dashed line roughly delimits the clear waters in the lagoon. Some sites in the English Harbor area have been omitted (cf. Fig. 2).

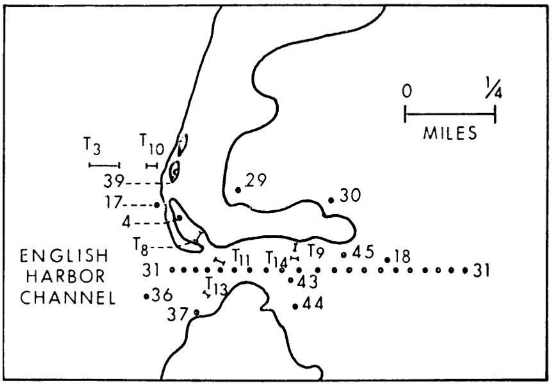


FIG. 2. Detail of English Harbor vicinity, all sample sites (numbered dots) and transect lines (short lines labeled $T_3$, $T_8$, etc.) included. Note Danger Point Tidepool (site 4, $T_8$) and Cartwright Point (between site 30 and site 45). Sample 31 was observed while it was drifting into the lagoon on a flood-tidal current.

The lagoon shoreline habitat, which almost completely surrounds the lagoon, is characteristically sand and sand-mud flats with varying algal and invertebrate cover (Kay and Switzer, this issue). The only relief features along most of the shoreline are occasional fallen coconut palms and rare limestone outcroppings. Essentially no live coral is present. The waters of this shallow zone are extremely turbid. Diver visibility was less than 60 cm vertically and 20 cm horizontally, perhaps because of the constant action of small wind waves.

Throughout much of the lagoon, diver visibilities ranged from 2–5 meters, due mostly to suspended particles of calcium carbonate (S. V. Smith, personal communication). This turbid portion of the lagoon topographically is a series of irregular "ponds" with sand-mud to soft mud bottoms, separated by extensive reticular reef formations. The linear reefs, along with various isolated coral knolls on pond edges and bottoms, form the turbid lagoon patch reef habitat. A more complete description is given by Maragos (1974*b*).

The remainder of the lagoon—the clear lagoon patch reefs—is subject to alternating tidal flows of clear open ocean and turbid lagoon waters passing through the English Harbor Channel (Fig. 1). Diver visibilities ranged from 2–15 m, varying with the tides and distance from the channel. The bottom is flat and sandy with relatively isolated coral formations; linear reefs are restricted to the outer margins of this habitat. Maragos (1974*b*) describes the corals and topography in greater detail.

The three channels connecting lagoon and open ocean differ from one another in depth and topography but all are characterized by rapid, nearly continual tidal currents. Current velocity in the most closely studied English Harbor Channel may exceed 5 knots in midchannel. Slack periods are very brief. The substrate distribution in English Harbor Channel is highly complex. The scoured limestone base in midchannel is overlain with rubble and large, boulderlike fragments, variously encrusted with corals and coralline algae. Toward the sides of the channel are larger heads of hard and soft corals and some loose sand, while the banks are loose shingle with a low algal cover.

The tidepool habitat, studied most intensely in the Danger Point Tidepool at the mouth of the English Harbor Channel (Figs. 2–3), has a flat, sandy bottom with considerable relief due to living hard and soft corals, limestone outcroppings, sand, shingle, and dead coral rubble. Although water is continuously exchanged with the open ocean, the tidepools are typically protected from wave action. A porous shingle rampart protects Danger Point Tidepool; extensive seaward reefs protect a broad, well-defined moat of tidepool habitat at North Pass and a smaller, less distinct area northeast of Rapa Pass.

The outer reef flats are limestone benches, 5–30 m wide and often backed by shingle berms, on which occur low reef corals, some rubble and shingle, and various low algae. The uppermost portions may be partially exposed by very low tides. Most impressive here were the strong surge and wave conditions, particularly at the seaward margins which often terminate in spur-and-groove surge channels.

The outer reef slope habitat was extensively studied only in the vicinity of the English Harbor Channel, on the leeward side of Fanning. Topography and corals in this region have been described by Maragos (1974*a*, *b*); it will suffice to mention that water depths ranged from 7–36 m, and that the slope was a continuous jumble of coral and rubble, containing infrequent, isolated patches of sand.

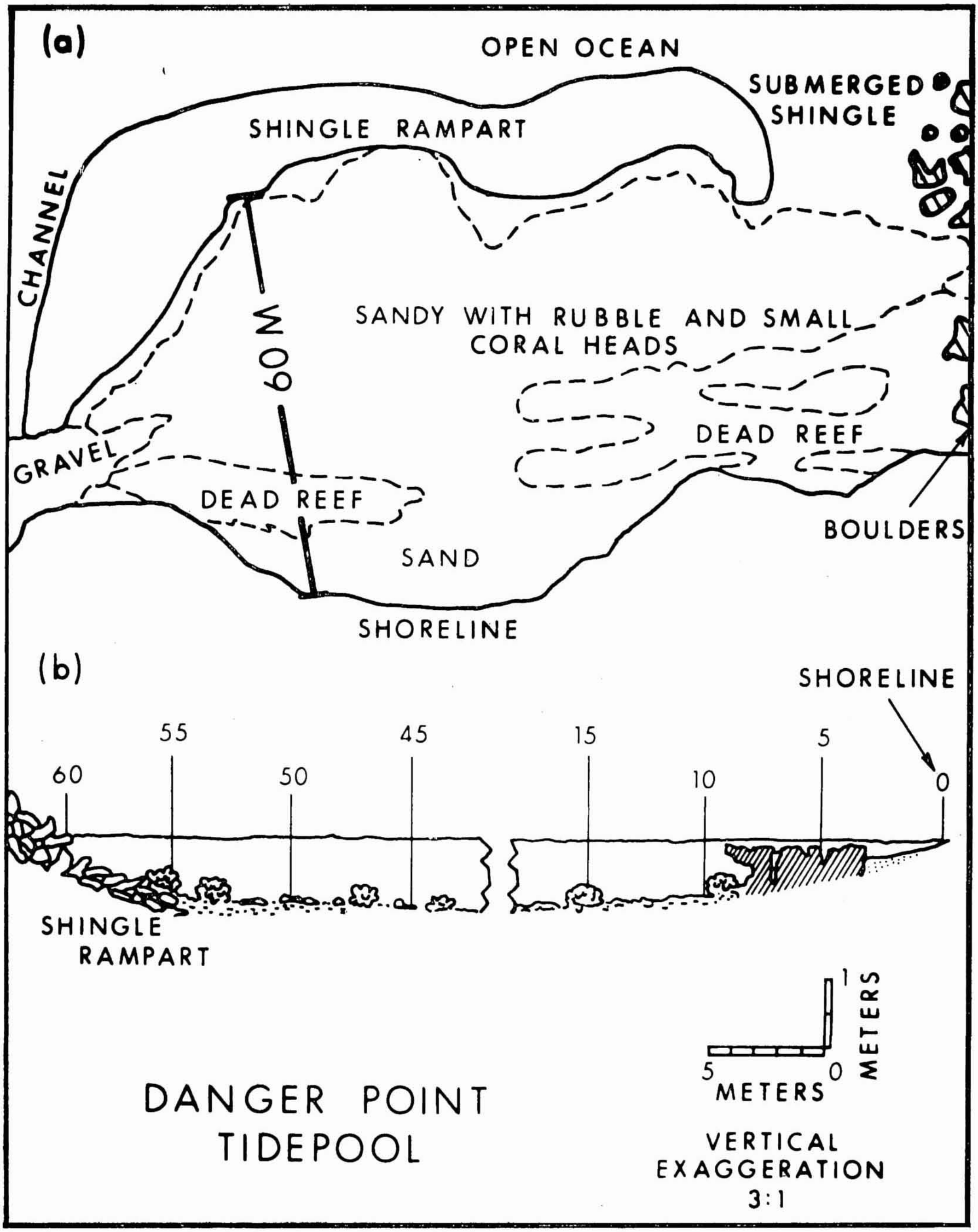


FIG. 3. Map of Danger Point Tidepool *a*, and bottom profile of 60 m $T_8$ transect *b*. Shallow passages over submerged shingle (*a*, upper left) and gravel riffles (*a*, far left) exposed only at extremely low tides.

*Field Methods*

Observations were made by SCUBA and free diving and recorded underwater on slates and film. Fishes were identified in the field from the descriptions of Schultz et al. (1953–1966), Randall (1955), and Gosline (1970). We photographed and where possible captured specimens with quinaldine, rotenone, spears, and nets for later identification of species which we could not recognize.

Qualitative (species) lists and abundance estimates were made at the sites numbered in Figs. 1 and 3. Quantitative records were made along eight transects traversed during July–August 1972 ($T_{1-8}$), and six during April 1973 ($T_{9-14}$). Polypropylene lines with numbered lead weights at 1-m intervals were placed perpendicular to local depth contours. Two divers, one on either side of the line, noted the species and numbers of fishes present within 1.5 m on either side of the line and within 3 m of the bottom, in 5-m increments along the line. Each transect was thus a contiguous series of 45 $m^3$ sample "stations."

Nearly 14 hours were spent observing the fishes of the turbid lagoon patch reefs. During this time one 100-m transect ($T_2$) and two 20-m transects ($T_4$, $T_7$) were traversed. Corresponding figures for the other habitats are: clear lagoon patch reefs—10½ hours, one 100-m transect ($T_1$) and two 20-m transects ($T_5$, $T_6$); channel habitat—16 hours, four 20-m transects in the English Harbor Channel ($T_9$, $T_{11}$, $T_{13}$, $T_{14}$); tidepool habitat—7 hours, one 60-m transect in the Danger Point Tidepool ($T_8$); outer reef flats—6½ hours, two 20-m transects along the lee shore ($T_{10}$, $T_{12}$); outer reef slope habitat—7 hours, one 100-m transect ($T_3$), also on the lee side. The extreme turbidity along the lagoon shoreline precluded underwater observation. Species recorded for this habitat were observed from above the surface—2½ hours walking and wading along the shoreline; no quantitative data were obtained.

*Analysis*

We were unable to expend an equal amount of sampling time and effort in each habitat. Our samples were, however, too small to reduce further with Sanders' rarefaction technique for comparing samples of unequal size (Sanders 1968; see also Fager's (1972) critique of this method). Furthermore, we repeatedly observed certain species that avoided the transect lines. We therefore used the quantitative (transect) data and subjective abundance estimates together to assign an abundance rank to each species for every habitat in which it occurred. Abundance ranks were then valued by the minimum number of individuals per study site attaining that rank: ratings of "abundant" were coded 20; "common," 5; and "occasional," 2 (see Table 1 for density equivalents). We based our analysis on these semiquantitative, coded ranks. We excluded rankings of "rare," which indicate only one sighting of one individual of the particular species in the given habitat, from further consideration. Also omitted were the carangid fishes, since only one species could be identified with any certainty.

Diversities in bits per "individual" were calculated with Brillouin's formula (Pielou 1966) from the coded abundance scores for each habitat. Values of faunal resemblance for each possible pair of habitats were estimated by two measures. The simple matching coefficient (Sokal and Sneath 1963), which equals unity less the relative distance quantity advocated by Blackith and Reyment (1971), utilizes only presence/absence information. Morisita's index, as modified by Horn (1966) for sampling with replacement, exploits also quantitative information contained in the data.

Raw counts of fishes and corals on the 100-m transects in the clear lagoon ($T_1$), turbid lagoon ($T_2$), and outer reef slope habitats ($T_3$) were used to produce species-species correlation matrices. We used Pearson product-moment correlation coefficients, although the occurrence data were clearly nonnormal in distribution; it was suggested to us that the Pearson $r$ is sufficiently robust to withstand such use (S. V. Smith, personal communication). Only those organisms positively correlated at or above the 0.5 level are mentioned below.

Such use of a parametric technique yields only a numerical index and not a sample statistic (Sokal and Rohlf 1969). For this reason, and because all of our indices are presented for hypothesis generation rather than testing,

TABLE 1

ESTIMATES OF ABUNDANCE AND DISTRIBUTIONS OF FISHES AMONG HABITATS

| TAXA | LAGOON SHORE-LINE | TURBID LAGOON PATCH REEFS | CLEAR LAGOON PATCH REEFS | CHANNEL | TIDE-POOLS | OUTER REEF FLAT | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| ALBULIDAE | | | | | | | |
| *Albula vulpes* (Linn.) | O | | | | | O | |
| MURAENIDAE | | | | | | | |
| *Gymnothorax flavimarginatus* (Rüppell) | | | | | R | | |
| *G. javanicus* (Bleeker) | | | | | R | | |
| *G. margaritophorus* Bleeker | | | | R | | | |
| *G. pictus* (Ahl) | | | | | R | O | |
| *G. undulatus* (Lacépède) | | | | | | R | R |
| CHANIDAE | | | | | | | |
| *Chanos chanos* (Forsskål) | C | | C | | | O | O |
| EXOCOETIDAE | | | | | | | |
| *Hyporhamphus acutus* (Günther) | | | C | C | C | C | C |
| BELONIDAE | | | | | | | |
| *Belone platyura* Bennett | | | | | C | C | C |
| HOLOCENTRIDAE | | | | | | | |
| *Adioryx caudimaculus* (Rüppell) | | | | R | | | |
| *A. lacteoguttatus* (Cuv.) | | | O | | | | |
| *A. microstomus* (Günther) | | | | | O | | |
| *A. spinifer* (Forsskål) | | | | | O | | O |
| *A. tiere* (Cuv. & Val.) | | | | | | | R |
| *A. tieroides* (Bleeker) | | | | | | | R |
| *Flammeo sammara* (Forsskål) | | | | | O | | |
| *Myripristis amaenus* Castelnau* | | R | O | | | | |
| *M. kuntee* (Cuv. & Val.) | | R | O | | | | A |
| *M. murdjan* Forsskål* | | | | | | | A |
| FISTULARIIDAE | | | | | | | |
| *Fistularia petimba* Lacépède | | | | R | | | |
| SYNGNATHIDAE | | | | | | | |
| *Doryrhamphus melanopleura* (Bleeker) | | | | | R | R | |
| SCORPAENIDAE | | | | | | | |
| *Scorpaena albobrunnea* Günther | | | | | O | | |
| CARACANTHIDAE | | | | | | | |
| *Caracanthus maculatus* (Gray) | | | | | O | O | O |
| SERRANIDAE | | | | | | | |
| *Cephalopholis argus* Bloch & Schneider | | R | O | O | O | | A |
| *C. urodelus* (Bloch & Schneider) | | R | O | O | R | | O |
| *Epinephelus coralicola* Cuv. & Val. | | | | | R | | |
| *E. fasciatus* (Forsskål) | | | R | | | | R |
| *E. fuscoguttatus* (Forsskål) | | R | O | O | O | | O |
| *E. hexagonatus* (Bloch & Schneider) | | R | | | O | R | O |
| *E. merra* Bloch | R | O | C | O | C | O | R |
| *E. spilotoceps* Schultz | | | R | O | O | O | O |
| *Gracila albimarginata* (Fowler & Bean) | | | | | | | O |
| *Mirolabrichthys* sp.† | | | | | | | A |
| *Pseudanthias* undescr. sp.† | | | | | | | A |
| *Variola louti* (Forsskål) | | | | R | | | O |

TABLE 1 (*cont.*)

| TAXA | LAGOON SHORE-LINE | TURBID LAGOON PATCH REEFS | CLEAR LAGOON PATCH REEFS | CHANNEL | TIDE-POOLS | OUTER REEF FLAT | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| PSEUDOCHROMIDAE | | | | | | | |
| *Pseudogramma polyacantha* (Bleeker) | | | | | | | R |
| APOGONIDAE | | | | | | | |
| *Apogon erythrinus* Snyder | | | | | O | | |
| *A. frenatus* Val. | | | O | | | | |
| *A. novemfasciatus* Cuv. & Val. | | | | | | O | |
| *A. robustus* (Smith & Radcliffe) | | | O | | R | | |
| *A. savayensis* Günther | | | | | O | | |
| *A. snyderi* Jordan & Evermann | | | | | R | | |
| *Cheilodipterus quinquelineata* Cuv. & Val. | | C | O | | | | |
| BRANCHIOSTEGIDAE | | | | | | | |
| *Malacanthus latovittatus* (Lacépède) | | | O | O | | | R |
| CARANGIDAE | | | | | | | |
| *Caranx ignobilis* (Forsskål) | | | | O | | O | |
| *C. lugubris* Poey | | O | | | O | | |
| *C. melampygus* Cuv. & Val. | | | O | O | O | O | O |
| *C. sexfasciatus* Quoy & Gaimard | | O | R | | | | |
| *Gnathodon speciosus* (Forsskål) | | O | R | | | | |
| *Scomberoides lysan* Forsskål | | O | O | O | | | O |
| *Trachinotus bailloni* (Lacépède) | | | | | O | O | |
| LUTJANIDAE | | | | | | | |
| *Aphareus furcatus* (Lacépède) | | | | | | | R |
| *Caesio xanthonotus* Bleeker | | | | | | | A |
| *Lethrinus xanthocheilus* Klunzinger | | | R | O | | O | O |
| *Lutjanus bohar* (Forsskål) | | | R | O | | | C |
| *L. fulvus* (Bloch & Schneider) | C | C | O | | C | R | |
| *L. gibbus* (Forsskål) | | | | O | R | R | O |
| *L. monostigma* (Cuv. & Val.) | O | | R | O | O | | O |
| SPARIDAE | | | | | | | |
| *Gnathodentex aureolineatus* (Lacépède) | | | O | | | | |
| *Monotaxis grandoculis* (Forsskål) | | O | O | O | O | | O |
| MULLIDAE | | | | | | | |
| *Mulloidichthys flavolineata* (Lacépède) | O | | | | A | | |
| *M. samoensis* (Günther) | | | | | C | | |
| *Parupeneus barberinus* (Lacépède) | O | O | O | C | O | R | |
| *P. bifasciatus* (Lacépède) | | | R | C | | | |
| *P. multifasciatus* (Quoy & Gaimard) | | R | O | O | O | | R |
| *P. pleurostigma* (Bennett) | | | | O | | | |
| *P. porphyreus* (Jenkens) | | | | R | | | R |
| PEMPHERIDAE | | | | | | | |
| *Pempheris oualensis* Cuv. & Val. | | | | | | | R |

TABLE 1 (*cont.*)

| TAXA | LAGOON SHORE-LINE | TURBID LAGOON PATCH REEFS | CLEAR LAGOON PATCH REEFS | CHANNEL | TIDE-POOLS | OUTER REEF FLAT | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| KYPHOSIDAE | | | | | | | |
| *Kyphosus cinerascens* (Forsskål) | | | | | | O | |
| CHAETODONTIDAE | | | | | | | |
| *Centropyge flavissimus* (Cuv.) | | | C | C | R | O | C |
| *C. loriculus* (Günther) | | | | | | | O |
| *Chaetodon auriga* Forsskål | R | O | O | O | O | O | C |
| *C. bennetti* Cuv. | | R | O | R | R | | O |
| *C. ephippium* Cuv. | | R | O | O | O | | O |
| *C. lineolatus* Cuv. | | | R | R | | | O |
| *C. lunula* (Lacépède) | R | O | O | C | O | R | O |
| *C. myeri* Bloch & Schneider | | | | | | | O |
| *C. ornatissimus* Cuv. & Schneider | | | O | O | R | | C |
| *C. punctatofasciatus* Cuv. & Val. | | | | | | | O |
| *C. quadrimaculatus* Gray | | | | O | | | |
| *C. reticulatus* Cuv. | | | | | | | R |
| *C. semion* Bleeker | | | O | | | | |
| *C. trisfasciatus* Mungo Park | | O | O | | R | | O |
| *C. ulietensis* Cuv. & Val.‡ | | | O | R | | | O |
| *C. vagabundus* Linn. | | O | | | | | |
| *Holocanthus* undescr. sp.§ | | | | O | | | R |
| *Megaprotodon trifascialis* (Gmelin) | | | O | R | R | | O |
| *Pomacanthus imperator* Bloch | | | | R | | | O |
| POMACENTRIDAE | | | | | | | |
| *Abudefduf dicki* (Lienard) | | R | O | C | O | C | A |
| *A. glaucus* (Cuv. & Val.) | O | | R | O | A | A | |
| *A. imparipennis* (Vaillant & Sauvage) | | | | O | R | C | O |
| *A. septemfasciatus* (Cuv. & Val.) | R | | | R | O | C | |
| *A. sordidus* (Forsskål) | O | | | C | O | O | |
| *Chromis acares* Randall & Swerdloff | | | | | | | A |
| *C. atripectoralis* Welander & Schultz | | A | O | | | | |
| *C. lepidolepis* Bleeker | | | C | O | | | |
| *C. margaritifer* Fowler | | | O | C | O | | A |
| *C. vanderbilti* (Fowler) | | | | O | | R | A |
| *Dascyllus aruanus* (Linn.) | | C | A | R | A | | |
| *Dascyllus* undescr. sp.§ | | O | O | | R | | |
| *Plectroglyphidodon johnstonianus* Fowler & Ball | | | | | | R | C |
| *Pomacentrus albofasciatus* Schlegel & Müller | O | C | A | A | A | O | |
| *P. aureus* Fowler | | | | C | | C | |
| *P. coelestis* Jordan & Starks | | R | A | A | O | C | O |
| *P. lividus* (Bloch & Schneider) | | A | A | O | A | | |
| *P. nigricans* (Lacépède) | | O | A | | A | | |
| *Pomacentrus* sp.§ | | | | | | | O |
| *P. vaiuli* Jordan & Seale | | | | | | O | O |
| CIRRHITIDAE | | | | | | | |
| *Cirrhitichthys oyxcephalus* (Bleeker) | | | C | O | O | O | O |
| *Paracirrhites arcatus* (Cuv. & Val.) | | | | O | R | | O |

Table 1 (*cont.*)

| TAXA | LAGOON SHORE-LINE | TURBID LAGOON PATCH REEFS | CLEAR LAGOON PATCH REEFS | CHANNEL | TIDE-POOLS | OUTER REEF FLAT | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| CIRRHITIDAE (*cont.*) | | | | | | | |
| *P. forsteri* (Bloch & Schneider) | | | R | O | R | | C |
| *P. hemistictus* (Günther) | | | | R | | | O |
| *P. polystictus* (Günther) | | | | R | | | |
| MUGILIDAE | | | | | | | |
| *Chelon vaigiensis* (Quoy & Gaimard) | C | | | | C | O | |
| *Crenimugil crenilabis* (Forsskål) | C | | O | | A | C | |
| SPHYRAENIDAE | | | | | | | |
| *Sphyraena forsteri* Cuv. & Val. | | | | | | | O |
| LABRIDAE | | | | | | | |
| *Anampses chrysocephalus* Randall | | | | R | | | |
| *Bodianus axillaris* (Bennett) | | | | | | | O |
| *B. diana* (Lacépède) | | | | | | | O |
| *B. loxozonus* (Snyder)‖ | | | | O | | R | C |
| *Cheilinus rhodocrous* Günther | | | | | | | R |
| *C. undulatus* Rüppell | | R | O | O | O | O | O |
| *Cirrhilabrus temmincki* Bleeker | | | O | O | R | | |
| *Cirrhilabrus* undescr. sp. | | | | O | | | |
| *Coris aygula* Lacépède | | | | O | O | | |
| *C. ballieui* Vaillant & Sauvage | | | | R | | | |
| *C. gaimardi* (Quoy & Gaimard) | | | R | O | R | | |
| *Epibulus insidiator* (Pallas) | | R | O | | R | R | O |
| *Gomphosus varius* Lacépède | | C | O | O | O | O | C |
| *Halichoeres centriquadrus* (Lacépède) | | | R | C | O | O | |
| *H. margaritaceus* (Cuv. & Val.) | | | | O | O | A | |
| *H. trimaculatus* (Quoy & Gaimard) | O | A | A | A | A | O | O |
| *Hemigymnus fasciatus* (Bloch) | | | | O | | | O |
| *Hemipteronotus leclusei* (Quoy & Gaimard) | | | R | O | | | |
| *H. taeniourus* (Lacépède) | | | | O | R | | |
| *Labroides bicolor* Fowler & Bean | | | R | R | R | | O |
| *L. dimidiatus* (Cuv. & Val.) | | O | C | C | O | O | C |
| *L. rubrolabiatus* Randall | | | R | | R | R | A |
| *Pseudocheilinus hexataenia* (Bleeker) | | R | O | O | O | O | A |
| *Pseudocheilinus* sp.§ | | | | R | | | A |
| *Stethojulis balteatus* (Quoy & Gaimard) | | | | C | O | O | |
| *S. linearis* Schultz | | | | O | R | O | R |
| *Thalassoma amblycephalus* (Bleeker) | | O | A | A | A | C | O |
| *T. hardwickei* (Bennett) | | | | R | O | O | |
| *T. lunare* (Linn.) | | C | A | C | O | O | |
| *T. lutescens* (Lay & Bennett) | | | | R | | | O |
| *T. purpureum* (Forsskål) | O | O | O | O | O | A | |
| *T. quinquevittata* (Lay & Bennett) | | O | O | A | O | | |
| SCARIDAE | | | | | | | |
| *Chlorurus gibbus* (Rüppell) | | O | O | C | O | O | A |
| *Scarus "brevifillis"*# | | R | R | O | | O | O |
| *S. chlorodon* Jenyns | | | R | | | | O |
| *S. forsteri* Cuv. & Val. | | | | R | | R | O |
| *S. "frenatus"*** | | | | O | O | O | R |

Table 1 (*cont.*)

| TAXA | LAGOON SHORE-LINE | TURBID LAGOON PATCH REEFS | CLEAR LAGOON PATCH REEFS | CHANNEL | TIDE-POOLS | OUTER REEF FLAT | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| SCARIDAE (*cont.*) | | | | | | | |
| *S. ghobban* (Forsskål) | | | O | C | O | O | O |
| *S. globiceps* Cuv. & Val. | | | O | O | O | | O |
| *S. harid* Forsskål | R | O | O | C | C | C | O |
| *S. jonesi* (Streets) | | | O | C | C | C | O |
| *S. oviceps* Cuv. & Val. | | O | O | R | O | O | O |
| *S. "pectoralis"*†† | | O | R | O | | O | |
| *S. sexvittatus* Rüppell | | | R | O | O | R | |
| *S. sordidus* Forsskål | | A | O | O | R | R | R |
| juvenile scarids | O | C | O | O | O | R | |
| MUGILOIDIDAE | | | | | | | |
| *Parapercis cephalopunctatus* (Seale) | | | | O | | | |
| BLENNIIDAE | | | | | | | |
| *Aspidontus taeniatus* Quoy & Gaimard‖ | | | | | | | O |
| *Cirripectes sebae* (Cuv. & Val.) | | | | O | O | R | O |
| *C. variolosus* (Cuv. & Val.) | | | | | O | C | O |
| *Cirripectes* undescr. sp.† | | | O | | | | |
| *Entomacrodus striatus* (Quoy & Gaimard) | | | | | O | O | |
| *Istiblennius afilinuchalis* Schultz & Chapman | | | | | | O | |
| *I. edentulus* (Bloch & Schneider) | | | | | C | | |
| *I. lineatus* (Cuv. & Val.) | | | | | O | O | |
| *I. paulus* (Bryan & Herre) | | | | O | C | C | |
| *Plagiotremus tapeinosoma* (Bleeker) | | R | O | O | O | R | |
| TRIPTERYGIIDAE | | | | | | | |
| *Helcogramma* undescr. sp. †, ‡‡ | | | | O | | | |
| *Tripterygion minutus* Günther | | | | O | R | | |
| GOBIIDAE | | | | | | | |
| *Amblygobius albimaculatus* (Rüppell) | | C | O | | | | R |
| *Asterropteryx semipunctatus* Rüppell | | C | O | | | | |
| *Bathygobius fuscus* (Rüppell) | | | | | R | | |
| *Eleotrides strigata* (Bleeker) | | | O | O | O | | R |
| *Eviota distigma* Rüppell | | O | C | C | C | | |
| *Fusigobius neophytus* (Günther) | | O | O | O | O | | |
| *Gnatholepis anjerensis* (Bleeker) | | O | C | C | C | | R |
| *Paragobiodon echinocephalus* (Cuv. & Val.) | | R | | | C | C | |
| *Ptereleotris microlepis* (Bleeker) | | | O | O | | | R |
| *Ptereleotris* sp.§§ | | | | | | | R |
| *Quisquilius naraharae* (Snyder) | | R | O | | | | |
| *Trimma* sp.† | | | | O | | | |
| ACANTHURIDAE | | | | | | | |
| *Acanthurus achilles* Shaw | | | | O | | O | |
| *A. gahhm* (Forsskål) | R | R | C | A | C | R | O |
| *A. glaucoparieus* Cuv. | | | | C | O | C | A |
| *A. guttatus* Bloch & Schneider | | | | | | O | |
| *A. lineatus* (Linn.) | | | | O | O | A | O |
| *A. olivaceus* Bloch & Schneider | | | | A | | | |
| *A. triostegus* (Linn.) | O | O | C | A | A | A | |
| *A. xanthopterus* Cuv. & Val. | O | O | C | O | R | O | C |
| *Ctenochaetus cyanoguttatus* Randall | | | | C | | O | C |
| *C. striatus* (Quoy & Gaimard) | | O | O | A | C | A | A |

Table 1 (*cont.*)

| TAXA | LAGOON SHORE-LINE | TURBID LAGOON PATCH REEFS | CLEAR LAGOON PATCH REEFS | CHANNEL | TIDE POOLS | OUTER REEF FLAT | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| ACANTHURIDAE (*cont.*) | | | | | | | |
| *Ctenochaetus* sp.§ | | | | R | | | R |
| *Naso brevirostris* (Val.) | | | | O | O | | O |
| *Paracanthurus hepatus* (Linn.) | | | | O | | | |
| *Zanclus canescens* (Linn.) | | | R | O | | R | O |
| *Zebrasoma rostratum* (Günther) | | | | | | O | O |
| *Z. veliferum* (Bloch) | | O | O | O | O | | O |
| PLEURONECTIDAE | | | | | | | |
| *Samariscus triocelatus* Woods | O | | | | | | |
| BALISTIDAE | | | | | | | |
| *Balistapus undulatus* (Mungo Park) | | | R | O | O | R | O |
| *Balistoides viridescens* (Bloch & Schneider) | | | | O | | | |
| *Melichthys niger* (Bloch) | | | | | | O | O |
| *M. vidua* (Solander) | | | | R | | | |
| *Rhinecanthus aculeatus* (Linn.) | O | O | O | O | O | | |
| R. *rectangulus* (Bloch & Schneider) | | | R | | R | C | |
| monacanthid sp. | | | | | | | O |
| TETRAODONTIDAE | | | | | | | |
| *Arothron hispidus* (Linn.) | O | | | O | | | |
| *A. meleagris* (Lacépède) | R | R | R | O | O | R | O |

NOTE: A, abundant (more than 19 individuals/site or more than 1.7 individuals/station); C, common (more than 4 and less than 20 individuals/site or more than 0.4 and less than 1.8 individuals/station); O, occasional (more than 1 and less than 5 individuals/site or less than 0.5 individuals/station); R, rare (1 individual per site or entire transect).

* Greenfield, in press.

† Specimen(s) placed in the Bernice P. Bishop Museum, Honolulu, Hawaii.

‡ *Chaetodon falcula* = *C. ulietensis* (W. C. Burgess, personal communication).

§ Photograph available. || J. E. Randall (personal communication). In regard to *Aspidontus taeniatus* Quoy & Gaimard, see Smith-Vaniz and Randall (1973).

\# *Scarus brevifillis* (Günther) is the female form of *S. chlorodon* Jenyns (Randall 1963).

** *Scarus frenatus* Lacépède is the male form of *S. sexvittatus* Rüppell (Randall 1963).

†† *Scarus pectoralis* Cuv. & Val. is the male form of *S. oviceps* Cuv. & Val. (Randall 1963).

‡‡ R. R. Rosenblatt (personal communication); specimens also at Scripps Institute of Oceanography, La Jolla, California.

§§ Individual like *Ptereleotris microlepis* but margin of caudal with short, dark, horizontal stripes.

confidence limits are inappropriate (Sokal and Rohlf 1969, Pielou 1972).

## RESULTS

We found 214 species of nearshore marine fishes (96 genera in 37 families) at Fanning Island. The species and their abundance ranks in each of the seven habitats are listed systematically in Table 1. Species assemblages characteristically observed over particular substrates within the habitats are presented in Table 2.

Fourteen species ranged widely throughout most of the habitats. *Chlorurus gibbus*, a large scarid, was absent only from the lagoon shoreline. *Halichoeres trimaculatus* and *Acanthurus xanthopterus*, wrasse and surgeonfish respectively, were seen over the edges of sand patches near outcroppings of live coral and dead reef in all seven habitats. The other widely ranging species were associated with particular kinds of substrate and were rare in, or absent from, either the lagoon shoreline or the outer reef slopes: *Epinephelus merra*, *Pomacentrus albofasciatus*, *Thalassoma purpureum*, *Scarus harid*, and *Acanthurus triostegus* were characteristic of shallow water

TABLE 2

DISTRIBUTIONS OF FISHES WITHIN HABITAT AREAS

A. LAGOON SHORELINE

1. MIDWATER SCHOOLS
*Chanos chanos*
*Chelon vaigiensis*
*Crenimugil crenilabis*

2. OVER SAND
*Albula vulpes*
*Mulloidichthys flavolineata*
*Parupeneus barberinus*
*Acanthurus triostegus*
*A. xanthopterus*
*Samariscus triocellatus*
*Arothron hispidus*

3. NEAR ROCKS
*Lutjanus fulvus*
*L. monostigma*
*Abudefduf glaucus*
*A. sordidus*
*Pomacentrus albofasciatus*
*Halichoeres trimaculatus*
*Thalassoma purpureum*
juvenile scarids
*Rhinecanthus aculeatus*

B. TURBID LAGOON PATCH REEFS

1. OVER SAND
*Parupeneus barberinus*
*Chlorurus gibbus*
*Scarus harid*
*Amblygobius albimaculatus*
*Asterropteryx semipunctatus*
*Acanthurus triostegus*
*A. xanthopterus*
*Rhinecanthus aculeatus*

2. PATCH REEF TOPS
*Monotaxis grandoculis*
*Chaetodon auriga*
*C. lunula*
*C. trifasciatus*
*C. vagabundus*
*Chromis atripectoralis*
*Dascyllus aruanus*
*Dascyllus* n. sp.
*Pomacentrus albofasciatus*
*P. lividus*
*P. nigricans*
*Gomphosus varius*
*Halichoeres trimaculatus*
*Labroides dimidiatus*
*Thalassoma amblycephalus*
*T. lunare*
*T. quinquevittata*
*T. purpureum*
*Chlorurus gibbus*
*Scarus oviceps*
*S. pectoralis*

B2 *continued*
*S. sordidus*
*Zebrasoma veliferum*

3. PATCH REEF SIDES
*Epinephelus merra*
*Cheilodipterus quinquelineata*
*Lutjanus fulvus*
*Chromis atripectoralis*
*Pomacentrus lividus*
*Gomphosus varius*
*Halichoeres trimaculatus*
*Thalassoma lunare*
*Chlorurus gibbus*
*Eviota distigma*
*Fusigobius neophytus*
*Gnatholepis anjerensis*
*Ctenochaetus striatus*

C. CLEAR LAGOON PATCH REEFS

1. OVER SAND
*Malacanthus latovittatus*
*Parupeneus barberinus*
*Amblygobius albimaculatus*
*Asterropteryx semipunctatus*
*Eleotrides strigata*
*Ptereleotris microlepis*
*Acanthurus xanthopterus*

2. AREAS OF CORAL AND RUBBLE
*Centropyge flavissimus*
*Abudefduf dicki*
*Chromis atripectoralis*
*C. lepidolepis*
*C. margaritifer*
*Dascyllus aruanus*
*Dascyllus* n. sp.
*Pomacentrus albofasciatus*
*P. coelestis*
*P. lividus*
*P. nigricans*
*Cirrhitichthys oxycephalus*
*Cirrhilabrus temmincki*
*Halichoeres trimaculatus*
*Labroides dimidiatus*
*Pseudocheilinus hexataenia*
*Thalassoma amblycephalus*
*Cirripectes* n. sp.
*Plagiotremus tapeinosoma*
*Eviota distigma*
*Fusigobius neophytus*
*Gnatholepis anjerensis*
*Quisquilius naraharae*
*Ctenochaetus striatus*

3. CREVICES AND CAVES
*Adioryx lacteoguttatus*
*Myripristis amaenus*
*M. kuntee*

TABLE 2 (*cont.*)

C3 *continued*

*Cephalopholis argus*
*C. urodelus*
*Epinephelus fuscoguttatus*
*E. merra*
*Apogon frenatus*
*A. robustus*
*Cheilodipterus quinquelineata*

4. ERRANT

*Chanos chanos* (midwater)
*Hyporhamphus acutus* (surface)
*Lutjanus fulvus*
*Gnathodentex aureolineatus*
*Monotaxis grandoculis*
*Parupeneus barberinus*
*P. multifasciatus*
*Chaetodon auriga*
*C. bennetti*
*C. ephippium*
*C. lunula*
*C. ornatissimus*
*C. semion*
*C. trifasciatus*
*C. ulietensis*
*Megaprotodon trifascialis*
*Pomacentrus* sp.
*Crenimugil crenilabis* (midwater)
*Cheilinus undulatus*
*Epibulus insidiator*
*Gomphosus varius*
*Halichoeres trimaculatus*
*Thalassoma amblycephalus*
*T. lunare*
*T. purpureum*
*T. quinquevittata*
*Chlorurus gibbus*
*Scarus ghobban*
*S. harid*
*S. jonesi*
*S. oviceps*
*S. sordidus*
juvenile scarids
*Acanthurus gahhm*
*A. triostegus*
*A. xanthopterus*
*Zebrasoma veliferum*
*Rhinecanthus aculeatus*

D. CHANNELS

1. OVER SAND

*Malacanthus latovittatus*
*Parupeneus multifasciatus*
*P. pleurostigma*
*Halichoeres trimaculatus*
*Hemipteronotus leclusei*
*Parapercis cephalopunctatus*
*Eleotrides strigata*
*Fusigobius neophytus*
*Ptereleotris microlepis*
*Balistoides viridescens*

D1 *continued*

*Rhinecanthus aculeatus*
*Arothron hispidus*

2. ON CORAL HEADS OR IN CREVICES

*Cephalopholis argus*
*C. urodelus*
*Epinephelus fuscoguttatus*
*E. merra*
*E. spilotoceps*
*Cirrhitichthys oxycephalus*
*Paracirrhites arcatus*
*P. forsteri*
*Pseudocheilinus hexataenia*

3. AREAS OF CORAL AND RUBBLE

*Monotaxis grandoculis*
*Centropyge flavissimus*
*Chaetodon auriga*
*C. ephippium*
*C. ornatissimus*
*C. quadrimaculatus*
*Holacanthus* n. sp.
*Abudefduf dicki*
*A. glaucus*
*A. imparipennis*
*A. sordidus*
*Chromis lepidolepis*
*C. margaritifer*
*C. vanderbilti*
*Pomacentrus albofasciatus*
*P. aureus*
*P. lividus*
*Bodianus loxozonus*
*Cirrhilabrus temmincki*
*Cirrhilabrus* n. sp.
*Coris aygula*
*C. gaimardi*
*Gomphosus varius*
*Halichoeres margaritaceus*
*H. trimaculatus*
*Hemigymnus fasciatus*
*Hemipteronotus taeniourus*
*Labroides dimidiatus*
*Stethojulis linearis*
*Chlorurus gibbus*
*Cirripectes sebea*
*Istiblennius paulus*
*Plagiotremus tapeinosoma*
*Helcogramma* n. sp.
*Tripterygion minutus*
*Eviota distigma*
*Gnatholepis anjerensis*
*Trimma* sp.
*Acanthurus triostegus*
*Ctenochaetus striatus*
*Ctenochaetus* sp.
*Zanclus canescens*
*Zebrasoma veliferum*
*Balistapus undulatus*

4. ERRANT

*Hyporhamphus acutus* (surface)
*Lethrinus xanthocheilus*

TABLE 2 (*cont.*)

D4 *continued*

*Lutjanus bohar*
*L. gibbus*
*L. monostigma*
*Parupeneus barberinus*
*P. bifasciatus*
*P. multifasciatus*
*Cheilinus undulatus*
*Halichoeres centriquadrus*
*Stethojulis axillaris*
*Thalassoma amblycephalus*
*T. lunare*
*T. purpureum*
*T. quinquevittata*
*Chlorurus gibbus*
*Scarus brevifillis*
*S. frenatus*
*S. ghobban*
*S. globiceps*
*S. harid*
*S. jonesi*
*S. pectoralis*
*S. sexvittatus*
*S. sordidus*
juvenile scarids
*Acanthurus achilles*
*A. gahhm*
*A. glaucopareius*
*A. lineatus*
*A. olivaceus*
*A. xanthopterus*
*Ctenochaetus cyanoguttatus*
*Paracanthurus hepatus*

E. TIDEPOOL

1. ALONG THE RUBBLE RAMPART

*Adioryx microstomus*
*Flammeo sammara*
*Epinephelus merra*
*Apogon erythrinus*
*A. savayensis*
*Lutjanus fulvus*
*Monotaxis grandoculis*
*Pomacentrus albofasciatus*
*Gomphosus varius*
*Halichoeres centriquadrus*
*H. trimaculatus*
*Labroides dimidiatus*
*Thalassoma hardwickei*
*T. quinquevittata*
*Chlorurus gibbus*
*Pomacentrus lividus*
*P. nigricans*
*Cirripectes sebae*
*C. variolosus*
juvenile scarids
*Acanthurus lineatus*
*A. triostegus*
*Ctenochaetus striatus*
*Ctenochaetus* sp.

2. CENTRAL SAND, CORAL, AND RUBBLE

*Hyporhamphus acutus*
*Belone platyura*
*Adioryx spinnifer*
*Scorpaena albobrunnea*
*Caracanthus maculatus*
*Cephalopholis argus*
*Epinephelus fuscoguttatus*
*E. hexagonatus*
*E. merra*
*E. spilotoceps*
*Mulloidichthys flavolineata*
*M. samoensis*
*Parupeneus barberinus*
*P. multifasciatus*
*Chaetodon auriga*
*C. ephippium*
*C. lunula*
*Abudefduf dicki*
*A. glaucus*
*Chromis margaritifer*
*Pomacentrus coelestis*
*P. lividus*
*P. nigricans*
*Cirrhitichthys oxycephalus*
*Chelon vaigiensis*
*Crenimugil crenilabis*
*Cheilinus undulatus*
*Coris aygula*
*Halichoeres margaritaceus*
*H. trimaculatus*
*Pseudocheilinus hexataenia*
*Stethojulis axillaris*
*Thalassoma amblycephalus*
*T. lunare*
*T. purpureum*
*Chlorurus gibbus*
*Scarus frenatus*
*S. ghobban*
*S. globiceps*
*S. harid*
*S. jonesi*
*S. oviceps*
*S. sexvittatus*
*Istiblennius edentulus*
*I. paulus*
*Plagiotremus tapaenisoma*
*Bathygobius fuscus*
*Eleotrides strigata*
*Eviota distigma*
*Fusigobius neophytus*
*Gnatholepis anjerensis*
*Paragobiodon echinocephalus*
*Acanthurus gahhm*
*A. glaucoparieus*
*A. triostegus*
*A. xanthopterus*
*Zebrasoma veliferum*
*Balistapus undulatus*
*Rhinecanthus aculeatus*
*Arothron meleagris*

TABLE 2 (*cont.*)

3. ALONG THE SANDY SHORELINE AND DEAD REEF
*Lutjanus monostigma*
*Abudefduf septemfasciatus*
*A. sordidus*
*Pomacentrus lividus*
*P. nigricans*
*Halichoeres trimaculatus*
*Entomacrodus striatus*
*Istiblennius edentulus*
*I. lineatus*
*Acanthurus triostegus*

F. REEF FLATS

1. FROM 0 TO 0.5 M DEPTH
*Gymnothorax pictus*
*Caracanthus maculatus*
*Epinephelus merra*
*E. spilotoceps*
*Apogon septemfasciatus*
*Abudefduf imparipennis*
*A. sordidus*
*Pomacentrus albofasciatus*
*P. coelestis*
*P. vaiuli*
*Cirrhitichthys oxycephalus*
*Gomphosus varius*
*Halichoeres centriquadrus*
*H. margaritaceus*
*H. trimaculatus*
*Thalassoma amblycephalus*
*T. hardwickei*
*T. lunare*
*T. purpureum*
*Scarus jonesi*
*Entomacrodus striatus*
*Istiblennius afilinuchalis*
*I. lineatus*
*I. paulus*
*Rhinecanthus rectangulus*

2. FROM 0.5 TO 3 M DEPTH
*Albula vulpes*
*Chanos chanos*
*Hyporhamphus acutus*
*Belone platyura*
*Kuhlia marginata*
*Lethrinus xanthocheilus*
*Kyphosus cinarescens*
*Centropyge flavissimus*
*Chaetodon auriga*
*Abudefduf dicki*
*Pomacentrus aureus*
*P. coelestis*
*Chelon vaigiensis*
*Crenimugil crenilabis*
*Cheilinus undulatus*
*Halichoeres margaritaceus*
*Labroides dimidiatus*
*Pseudocheilinus hexataenia*
*Stethojulis axillaris*
*S. linearis*

F2 *continued*
*Thalassoma purpureum*
*Chlorurus gibbus*
*Scarus brevifillis*
*S. frenatus*
*S. ghobban*
*S. harid*
*S. jonesi*
*S. oviceps*
*S. pectoralis*
*Cirripectes variolosus*
*Acanthurus achilles*
*A. glaucopareius*
*A. guttatus*
*A. lineatus*
*A. triostegus*
*A. xanthopterus*
*Ctenochaetus cyanoguttatus*
*C. striatus*
*Zebrasoma rostratum*
*Melichthys niger*

G. OUTER REEF SLOPE

1. OVER SAND
*Chanos chanos* (midwater)
*Halichoeres trimaculatus*
*Pomacentrus coelestis*
*Acanthurus xantheropterus*

2. ON OR WITHIN CORAL HEADS AND CAVES
*Adioryx spinnifer*
*Myripristis murdjan*
*Caracanthus maculatus*
*Cephalopholis argus*
*C. urodelus*
*Epinephelus fuscoguttatus*
*E. hexagonatus*
*E. spilotoceps*
*Cirrhitichthys oxycephalus*
*Paracirrhites arcatus*
*P. forsteri*
*P. hemistictus*
*Epibulus insidiator*
*Pseudocheilinus hexataenia*
*Pseudocheilinus* sp.
*Cirripectes variolosus*

3. NEAR ROCKS AND CORAL HEADS
*Myripristis kuntee*
*Cephalopholis argus*
*Mirolabrichthys* sp.
*Pseudanthias* sp.
*Centropyge flavissimus*
*C. loriculus*
*Chaetodon auriga*
*C. bennetti*
*C. ephippium*
*C. lineolatus*
*C. lunula*
*C. meyeri*
*C. ornatissimus*
*C. punctatofasciatus*
*C. trifasciatus*

TABLE 2 (*cont.*)

G3 *continued*
- *C. ulietensis*
- *Megaprotodon trifascialis*
- *Pomacanthus imperator*
- *Abudefduf dicki*
- *A. imparipennis*
- *Chromis acares*
- *C. lepidolepis*
- *C. margaritifer*
- *C. vanderbilti*
- *Plectroglyphidodon johnstonianus*
- *Pomacentrus vaiuli*
- *Bodianus axillaris*
- *B. diana*
- *Hemigymnus fasciatus*
- *Labroides bicolor*
- *L. dimidiatus*
- *Thalassoma amblycephalus*
- *T. lutescens*
- *Chlorurus gibbus*
- *Aspidontus taeniatus*
- *Ctenochaetus striatus*
- *Balistapus undulatus*
- *Melichthys niger*

4. ERRANT
- *Hyporhamphus acutus* (surface)
- *Belone platyura* (surface)
- *Gracila albimarginata*
- *Variola louti*

G4 *continued*
- *Caesio xanthonotus*
- *Lethrinus xanthocheilus*
- *Lutjanus bohar*
- *L. gibbus*
- *L. monostigma*
- *Monotaxis grandoculis*
- *Sphyraena forsteri*
- *Pomacentrus* sp.
- *Bodianus loxozonus*
- *Cheilinus undulatus*
- *Gomphosus varius*
- *Chlorurus gibbus*
- *Scarus brevifillis*
- *S. chlorodon*
- *S. forsteri*
- *S. ghobban*
- *S. globiceps*
- *S. harid*
- *S. jonesi*
- *S. oviceps*
- *Acanthurus gahhm*
- *A. glaucopareius*
- *A. lineatus*
- *A. xanthopterus*
- *Ctenochaetus cyanoguttatus*
- *Ctenochaetus* sp.
- *Zanclus canescens*
- *Zebrasoma rostratum*
- *Z. veliferum*
- *Arothron meleagris*

areas in which there was hard bottom with high relief; *Chaetodon auriga*, *C. lunula*, *Gomphosus varius*, *Labroides dimidiatus*, *Thalassoma amblycephalus*, and *Ctenochaetus striatus* were found always near living coral.

The lagoon shoreline habitat contained 19 species of occasional to abundant fishes, including six of the widely ranging species. The lagoon shoreline fauna was thus the smallest and least diverse (3.43 bits/individual; Table 4) of those sampled, and did not closely resemble that of any other habitat (Table 3).

Thirty-eight species were seen regularly on the turbid lagoon patch reefs, including all of the widely ranging species. Twenty-five species were recorded on the 20-m $T_7$ transect; 10 were represented by fewer than three individuals, and the diversity value for the entire turbid lagoon patch reef habitat was low (4.14 bits/individual). Among the more numerous fishes on $T_7$, 75 to 100 percent of the individuals of eight species, *Chielodipterus quinquelineata*, *Chaetodon vagabundus*, *Chromis atripectoralis*, *Dascyllus aruanus*, *Pomacentrus lividus*, *Scarus oviceps*, juvenile scarids, and *Ctenochaetus striatus*, were found with the corals *Acropora delicatula* and *A. formosa* on the sloping sides of the patch reefs. Elements of this assemblage also appeared on the 100-m $T_2$ transect: correlation coefficients greater than 0.5 suggest association of *Chromis atripectoralis* and *Pomacentrus lividus* with the two *Acropora* species. The small and relatively homogeneous turbid lagoon patch reef fish fauna was most similar to that of the adjacent clear lagoon patch reefs.

The clear lagoon patch reef habitat contained twice as many species (76) as were found in the turbid lagoon. The diversity was correspondingly higher (5.05 bits/individual). Data from all three clear lagoon transects indicate the co-occurrence of four abundant fish species: the damselfishes *Dascyllus aruanus* and *Pomacentrus coelestis* are associated with the wrasses *Halichoeres trimaculatus* and *Thalassoma lunare* ($r > 0.5$), but no statistical connection with particular environmental features could be made.

The English Harbor Channel habitat contained the most species (99) and had the highest

TABLE 3

MEASURES OF THE SIMILARITIES BETWEEN HABITAT-CHARACTERISTIC FAUNAS

*a*, SIMPLE MATCHING COEFFICIENTS OF ASSOCIATION

| LOCATION | LAGOON SHORELINE | TURBID LAGOON | CLEAR LAGOON | CHANNEL | TIDEPOOLS | OUTER REEF FLATS | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| Lagoon Shoreline | – | 0.19 | 0.13 | 0.11 | 0.16 | 0.15 | 0.03 |
| Turbid Lagoon | | – | 0.46 | 0.25 | 0.30 | 0.19 | 0.12 |
| Clear Lagoon | | | – | 0.40 | 0.42 | 0.23 | 0.29 |
| Channel | | | | – | 0.46 | 0.34 | 0.35 |
| Tidepools | | | | | – | 0.40 | 0.28 |
| Outer Reef Flats | | | | | | – | 0.28 |
| Means | 0.13 | 0.25 | 0.32 | 0.32 | 0.34 | 0.26 | 0.22 |

*b*, MORISITA'S INDICES OF OVERLAP

| LOCATION | LAGOON SHORELINE | TURBID LAGOON | CLEAR LAGOON | CHANNEL | TIDEPOOLS | OUTER REEF FLATS | OUTER REEF SLOPE |
|---|---|---|---|---|---|---|---|
| Lagoon Shoreline | – | 0.19 | 0.19 | 0.21 | 0.19 | 0.26 | 0.02 |
| Turbid Lagoon | | – | 0.52 | 0.27 | 0.07 | 0.10 | 0.05 |
| Clear Lagoon | | | – | 0.56 | 0.16 | 0.20 | 0.11 |
| Channel | | | | – | 0.40 | 0.50 | 0.23 |
| Tidepools | | | | | – | 0.73 | 0.55 |
| Outer Reef Flats | | | | | | – | 0.20 |
| Means | 0.18 | 0.20 | 0.29 | 0.36 | 0.35 | 0.33 | 0.19 |

NOTE: see text for details.

diversity (5.49 bits/individual) of the habitats sampled. The community structure was most closely approximated by the clear lagoon fish fauna (Table 3*b*). Many channel species also occurred in the smaller (83 species) Danger Point Tidepool fauna (Table 3*a*). The channel and tidepool habitats had the highest mean similarities to all other habitats, considering both species present and distributions of individuals among the species. Their fish faunas may thus be taken to best typify the fishes of Fanning Island.

The outer reef flat habitat supported fewer species of fish (64) than any other clear-water habitat. The diversity—4.90 bits/individual—was correspondingly low. The composition of the outer reef flat fish fauna most closely matched that of the tidepool habitat.

We found 91 species of fishes on the outer reef slope, but only 10 of the widely ranging species. Nineteen species of this diverse group (5.34 bits/individual) occurred in, at most, one other habitat. This substantial, unique component was reflected in the low mean indices of similarity (Table 3). Data obtained on the $T_3$ transect yielded correlation coefficients linking 19 fish species, 6 coral species, and at least 3 species of algae. The common-to-abundant fishes include *Myripristis kuntee*, *M. murdjan*, *Cephalopholis argus*, *Pseudanthias* sp., *Centropyge flavissimus*, *Chaetodon ornatissimus*, *Abudefduf dicki*, *Chromis margaritifer*, *C. vanderbilti*, *Plectroglyphidodon johnstonianus*, *Bodianus loxozonus*, *Gomphosus varius*, *Labroides dimidiatus*, *L. rubrolabiatus*, *Pseudocheilinus* sp., *Acanthurus glaucopareius*, *Ctenochaetus cyanoguttatus*, and *C. striatus*. These were associated with the corals *Acropora reticulata*, *Acropora* sp., *Favia stelligera*, *Lobophylla costata*, *Millepora platyphylla*, and *Pocillopora meandrina*; associated algae were *Dictyota friabilis*, *Lobophora variegata*, and coralline algae. Another association was observed, involving *Mirolabrichthys* sp. and *Chromis acares*, an anthiine serranid and a damselfish, and one species each of hermatypic and soft coral, *Leptastrea purpurea* and *Sarcophyton* sp. These two fishes were schooling plankton feeders, hovering above the corals and hiding among their branches when approached by us.

## DISCUSSION

The habitats as we have described them are not sharply defined. Wherever two habitats adjoin they intergrade to some degree. The border between turbid and clear lagoon waters, for example, depends on the amount of incoming, clear ocean water and thus on the tidal height at any given time; there is also some slight mixing. Changes in bottom topography are more persistent but form a gradual transition. From the premise that the distributional patterns of organisms reflect underlying variations of ecological parameters (Lambert and Dale 1964; implicit in the widely accepted concept of indicator organisms), it follows that since only 14 of the 214 species of fishes were seen more than once in at least six of the seven habitats, the Fanning nearshore marine environment is *not* homogeneous to reef fishes. We do not mean to imply that they necessarily respond to the particular factors by which we distinguished among habitats, but generally low coefficients of similarity suggest that the fishes did discriminate among our a priori habitats.

The most distinctive fish fauna was that of the lagoon shoreline. The low number of species present might derive from extreme turbidity and low sampling effort; however, the atypical natural and man-made relief features near Cartwright Point (sites 29 and 30, Fig. 2) may have caused inclusion of some fishes which do not occur in the more commonly barren portions. The two damselfishes *Abudefduf glaucus* and *A. sordidus*, for example, are listed in the lagoon shoreline fauna but were seen only along the shoreline at Cartwright Point. General paucity of species and high proportion (32 percent) but low number of widely ranging and presumably tolerant species suggest that the lagoon shoreline is relatively unsuitable for fish. Absence of living corals and other relief features probably has an important effect in reducing the fish fauna.

The small number of species is the major dissimilarity between the lagoon shoreline and other habitat faunas. Simple matching coefficients (Table 3*a*) show that adjacent turbid lagoon patch reefs held the greatest proportion of shoreline species. Table 3*b* reveals that, with respect to the distributions of individuals among the species present, the shoreline fauna was most similar (although not very) to the outer reef flat fauna. Reasons for this implied ecological similarity do not readily come to mind. Horn (1966) interprets Morisita's index as the probability of selecting two successive individuals of the same species from two samples [here habitat faunas] combined, relative to the probability of selecting two successive individuals of the same species from either of the samples alone. In this instance, in which the similarity of community structure (Morisita's index of overlap) exceeds the similarity based on the proportions of co-occurring species (simple matching coefficient), species which exist in high numbers in one habitat must also be relatively numerous in the other. Here, a large proportion (32 percent) of the shoreline species were widely ranging and all of these occurred on the reef flats.

Turbid lagoon patch reefs were much more heavily sampled than the shoreline and the probable accuracy of the turbid lagoon patch reef faunal list is much more reasonable. These fishes were most similar to those in the adjoining clear lagoon habitat and least similar to those in the turbulent outer reef flats and deeper reef slope. The marked discrepancies between overlap and simple matching measures of the similarities of turbid lagoon to tidepool fishes means that while many species were found in turbid lagoon *and* tidepool, they were not frequent in both. This relationship may reflect the preponderance of algal-encrusted rubble in the tidepool rather than live coral substrate, especially staghorn *Acropora*—as in the lagoon; or perhaps reflects strong tidal currents in the channel exerting a filtering effect on fishes that are not strong swimmers.

Faunistically, the clear lagoon patch reef habitat most nearly resembled the turbid lagoon patch reefs and channel habitat with which it merges. The relationship of lagoon fishes to tidepool fishes is much the same for turbid and clear lagoon. Both lagoon fish faunas also resembled the outer slope fauna much more closely in specific co-occurrence than in community structure.

The channel habitat had the fish fauna richest in species and diversity of the habitats we sampled. We believe that this was due in part to central location among habitat types, but due

TABLE 4

PROPERTIES OF THE HABITAT-CHARACTERISTIC FAUNAS

| LOCATION | NUMBER OF WIDELY RANGING SPECIES | TOTAL NUMBER OF SPECIES | ADJUSTED NUMBER OF INDIVIDUALS* | DIVERSITY (BITS PER INDIVIDUAL) |
|---|---|---|---|---|
| Lagoon Shoreline | 6 | 19 | 50 | 3.43 |
| Turbid Lagoon | 14 | 38 | 175 | 4.14 |
| Clear Lagoon | 14 | 76 | 329 | 5.05 |
| Channel | 14 | 99 | 441 | 5.49 |
| Tidepools | 13 | 83 | 391 | 5.21 |
| Outer Reef Flats | 13 | 64 | 284 | 4.90 |
| Outer Reef Slope | 10 | 91 | 509 | 5.34 |

NOTE: Data concerning carangids have been omitted because we could not identify these fishes to species with certainty.

* Adjusted number of individuals = sum of coded ranks for all of the abundant, common, and occasional species found in each habitat (details of coding in text); it thus underestimates the number of real fishes actually present.

to a greater degree to the remarkable variety of substrates in the channel. Many of the smaller species exploited protected microhabitats (Table 2D: 3 and 4), sheltering behind various projections from the strong tidal currents or keeping to the sides where currents were somewhat weaker. Such behavior, however, must reduce the mobility of these fishes and may impede travel between lagoon and seaward habitats. The importance of this hypothetical filtering effect might be tested at North Pass, where the channel is broad, shallow, and meandering. Other evidence of the effects of water movement is discussed below.

With respect to the distribution of individuals among species, the tidepools were very similar to outer reef slope and, to a lesser degree, to reef flats and channel habitats (Table 3*b*). This order may be partially attributable to our concentration on the conveniently located Danger Point Tidepool, smaller than the extensive moat of tidepool habitat at North Pass (sites 8–13, Fig. 1). The Danger Point Tidepool is open to both ocean and channel fishes (Fig. 3), but the seaward passage is wider and deeper. Thus, while individuals of many species may enter and survive, the limited space of Danger Point Tidepool is dominated by open ocean species.

The apparent paucity of fishes on the outer reef flats (Table 4) may also be partly artificial. We experienced considerable difficulty from wave turbulence and surge, and sampled relatively few sites on the reef flats. Nevertheless, the reef flat habitat probably supports fewer species than other clear-water habitats. This habitat continually contracts and expands with the tides. Protected microhabitats were few; there was little loose rubble or sand in which to burrow and wave washes rolled about the area. Measures of similarity between reef flats and slope were surprisingly low. We suspect considerable mixing of fish faunas in the zone between our deepest reef flat station (2 m) and our shallowest reef slope station (7 m), but were not able to sample there. If our data accurately represent existing similarities, the reef flat fauna was more closely allied to the channel fishes than to the outer reef slope. A possible explanation will be offered below.

The singular nature of the outer reef slope fish fauna, clearly not an artifact of impoverishment (Table 4), is manifest in the similarity values of Table 3. In fact, of 91 species on the outer reef slope, 36 or 40 percent were rare (sighted only once) or absent in all other habitats (compared to 21 of 99 "habitat-endemic" species in the channel). Two ecological features unique to the reef slopes are the constancy of water conditions characteristic of the open ocean, and depth. The average depth along the $T_3$ transect was 16 m; elsewhere at Fanning, only a few clear lagoon study sites (maximum depth 13 m) were even half as deep. The adjusted number of individuals was greater for the outer slope than in the channel where there were more species (Table 4) and many more study sites (Fig. 2). While other factors may have contributed to the greater number of fishes on the slope, the higher water column (i.e., depth) over the outer reef slope provided living space, food, and room to maneuver to some of the species not seen elsewhere.

As noted above, similarity measures associated the reef flats more closely with the channel than with the outer reef slope. Comparison of species co-occurrence similarity (simple matching coefficients) with community structure similarity (indices of overlap) indicates that individuals of species occurring both in the channel and on reef flats were numerous in both of these habitats, and that the opposite was true for fishes occurring in both channel and reef slope habitats. Comparison of the overlap between reef slope and tidepool faunas to their respective overlaps with the reef-flat fishes reveals that co-occurring species for the pair of calm-water habitats are much more frequent in these habitats than the fishes co-occurring in calm water-reef flat pairs of habitats are in those. That is, it would seem that species whose ranges include both reef slope and tidepool find these habitats more hospitable than the intervening reef flats. A similar system of relationships can be established for the outer reef slope, tidepool, and channel habitats although the channel is not situated between reef slope and tidepool. Implied in the sum of these relationships is a factor, shared by the channel and reef flats, which excludes reef slope and, to a lesser degree, tidepool fishes. Such a factor is strong water movement. It would seem to be an important determinant of the distributions of Fanning Island fishes, isolating the reef slope outside the turbulent reef flats and, to a lesser degree, containing the lagoon fishes with fast-flowing channel currents.

Within the seven habitats we found 214 species, 99 of which were not collected by Gosline (1970). Six are thought to be undescribed species and are under study by other workers, 29 had been previously reported from the Line Islands (Fowler 1928, 1931, 1934, 1949), and seven could not be identified to species. Table 1, then, includes the first published records for the Line Islands of 57 species. All of these but one are known to occur elsewhere in the central Pacific (Fowler 1928, 1931, 1934, 1949; Schultz 1943; Schultz and collaborators 1953–1966; Randall 1955). The exception, the wrasse *Coris ballieui*, has not been recorded previously outside of the Hawaiian Islands (Fowler 1928). Our observations are in complete accord with Gosline's (1971) characterization of the Line Islands fish fauna as "of the Central Pacific type as represented at the Marshall Islands" (p. 284).

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